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水份逆境對高粱生理性狀之影響

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摘　要

為探討高粱在生殖期間在缺水逆境下之生理反應，及其對產量影響，本試驗採用臺中5號及其親本2R與80B為材料。植株在孕穗期予以2、4或8天之斷水處理；試驗結果顯示：葉片之葉面積，葉綠素含量、可溶性蛋白質含量、硝酸還原酵素活性、澱粉含量和比葉重隨斷水處理時間加長而減少，NAR、預存物質含量、及乾物重亦呈現類似表現；然而，葉片總糖含量卻表現相反結果。不同品系在孕穗期經不同斷水處理之生理反應在各生育時期表現不一，品系在生育末期若能維持較高生理活性將有較大乾物重表現。

關鍵語：高粱、缺水逆境、生理反應、生殖生長期。

前　言

對大多數作物而言，生殖生長期間水份含量之高低，往往是造成產量降低之主要原因，缺水對作物之影響卻依作物之生育時期而定 (Ober et al., 1991)。高粱雖屬耐旱作物，在水份充份供應下其種子充實速率更佳 (Undersander, 1986)，然隨著田間灌溉時期不一，造成穗數、穗重表現亦有不同 (Grant et al., 1989；Hooker, 1985)。缺水造成植株乾物重、收穫指數及百粒重之降低(Sloane et al., 1990)，或因花與種子不育 (Cox and Jolliff, 1986；Grant et al., 1989)，或因植物生理活性衰退 (Frederick et al., 1990；Wolf et al., 1988) 所致。而不適當之水份供應影響植株生理狀況表現，諸如光合能力衰減 (Chaudhuri and Kanemasu, 1982；Seropian and Planchon, 1984)，硝酸還原酵素活性降低 (Chandra et al., 1983；Wolfe et al., 1988)等。在缺水情況下，引起高粱穀粒乾物降低敏感時期，有謂幼穗分化期(Ackerson et al., 1980)、抽穗期(Eck and Musick, 1979)、穀粒充實期 (Contsable and Hearn, 1978；Inuyama, 1980)等。本研究室未發表之報告指出水份在生殖生長期間之影響，尤以孕穗期為甚，其花粉粒活性不僅大大衰退，且種子充實期之發育亦受損甚重；說明高粱在生殖生長期間水份對產量之重要性。本試驗針對高粱在生殖生長期間水份對生理反應之影響作一探討，以確切明瞭影響小穗發育之生理性狀原因。

材料與方法

試驗材料：以高粱臺中五號及其親本80B與2R爲材料進行試驗。

試驗方法：試驗採盆栽方式，以內徑20公分、高30公分之陶盆，內裝混合土壤(風乾之分質壤土：泥碳土：珍珠石＝1：1：1)，利用張力計(tensiometer)控制土壤水分含量，並與土壤最大容水量90％(土壤有效水分約爲-0.15 MPa)相比較，使其維持土壤最大容水量之40％(土壤有效水分約爲-0.8 MPa)植株管理同一般田間管理，在孕穗期予以2、4及8天之斷水處理，採完全逢機設計，每次取樣三株。

調查項目：上述處理在生育期間進行下述項目之調查：

1. 葉面積：利用葉面積測定儀(LI-3100，美國Li-Cor公司產品)測定。
2. 葉綠素含量：葉片樣品經丙酮萃取過濾後，再依Arnon法(1959)測定。
3. 可溶性蛋白質含量：取酵素萃取液置於試管中，加入Bio-Rad試劑，利用Bio-Rad Protein分析法(1977)分析。
4. 葉片水勢：取10枚葉圓片(直徑1.96 cm^2)，利用HR-33T thermocouple psychrometer測定。
5. 硝酸還原酵素活性：將組織葉片置於反應液中，經水浴振盪，再加入含有sulfani- lamide及N-1-naphthylethylenediamine-HCl之亞硝酸反應液，依Jawerski法(Wolfe et al., 1988)分析。
6. 葉片溶質含量：利用電導度測定儀測定。
7. 葉莖與穀粒之全糖及澱粉之測定：將樣品乾燥磨粉後，利用anthrone法測定(Yoshida et al., 1972)。
8. 淨同化作用速率：計算單位時間內單位平均葉面積乾物重變化(Kvet et al., 1971)。

$$NAR=\frac{2(w2-w1)}{(A2+A1)(T2-T1)}$$

W1 : t1 取樣時乾重
W2 : t2 取樣時乾重
A1 : t1 葉面積
A2 : t2 葉面積
t1 : 第一次取樣時間
t2 : 第二次取樣時間

9. 農藝性狀調查。

結　　果

高粱植株在孕穗期不同斷水處理之葉片硝酸還原酵素活性示於圖1A；酵素活性隨斷水時間加長而降低，80B品系酵素活性隨生育期增加而減少。臺中5號在抽穗期及2R品系在乳熟期分別有較大之酵素活性表現。

葉片可溶性蛋白質含量示於圖1B；各品系斷水處理在乳熟期有最大可溶性蛋白質含量。在各生育期80B品系較其他品系含有較高之可溶性蛋白質含量。

葉綠素含量變化(圖1C)與硝酸還原酵素活性變化類似。

葉面積變化示於圖1D，圖中顯示各品系經不同斷水處理後葉面積表現，以斷水8天者最差，2R品系之葉面積經斷水後較其他品系大，且對照組及斷水2天在抽穗期呈現最大葉面積表現。

葉片總糖含量示於圖2A，各品系總糖含量隨斷水日數增加而增加，且在乳熟期達最高，斷水8天處理以臺中5號總糖含量最

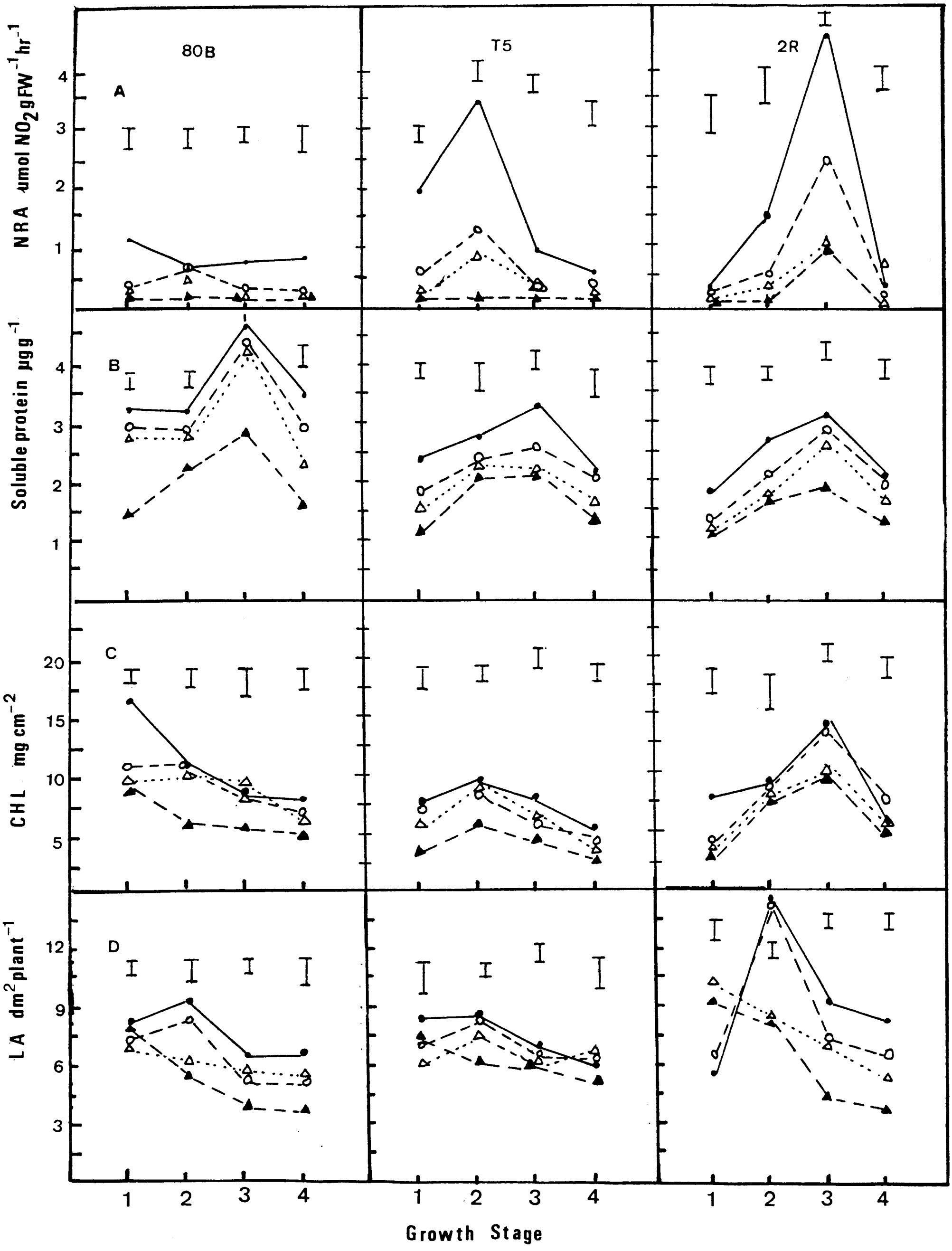

Fig 1. The leaf (A) nitrate reductase activity, (B) soluble protein contents, (C) chlorophyll contents and (D) leaf area of three sorghum genotypes undr water stress on different growth stage.

* ● control.

○ two days water stress treatment.

△ four days water stress treatment.

▲ eight days water stress treatment

** 1. Booting stage, 2. Headint stage, 3. Milk-repining stage, 4. Maturing stage.

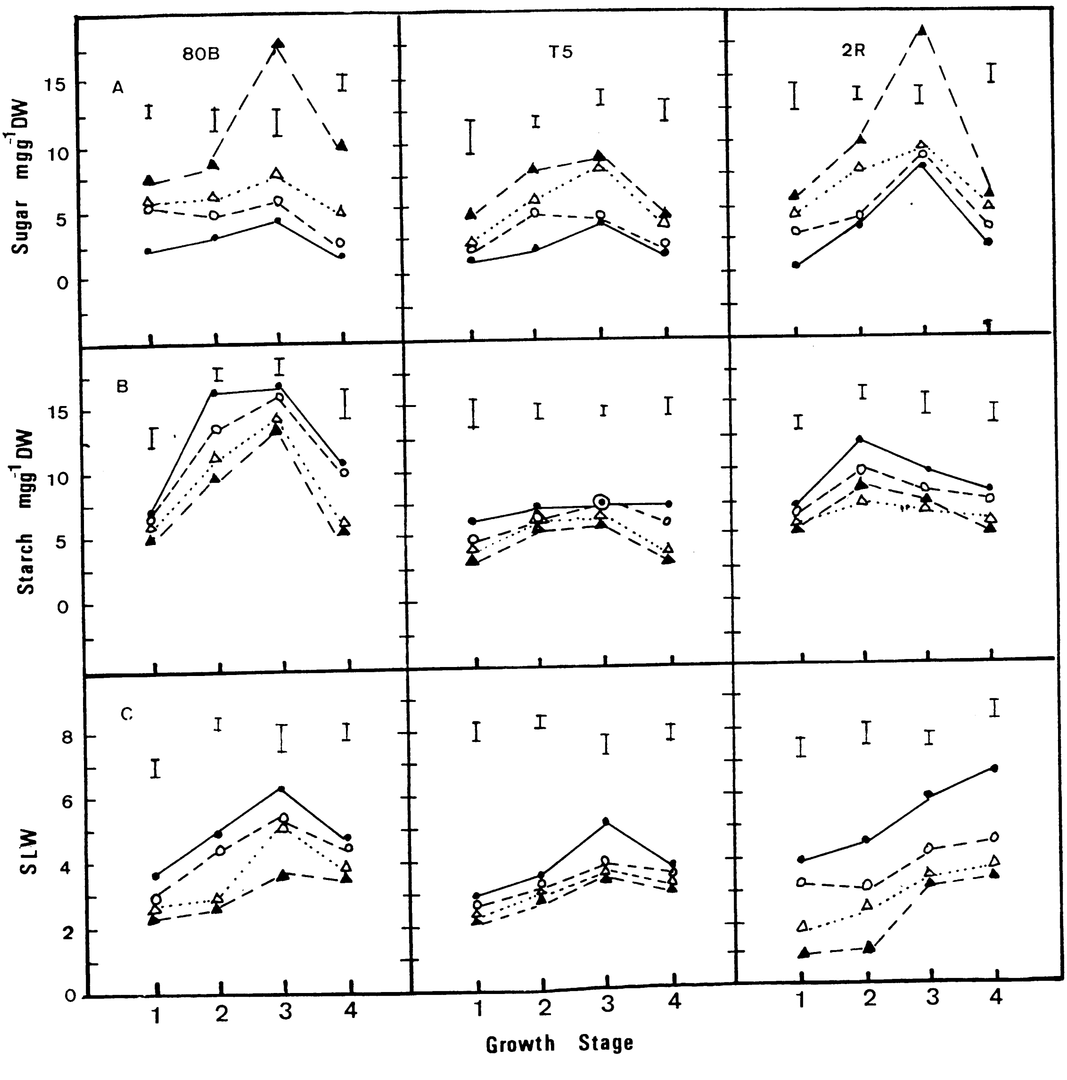

Fig 2. The leaf (A) total sugar contents, (B) starch contents, (C)specific leaf weight of three sorghum genotypes under water stress on different growth stages.

* ● control.

○ two days water stress treatment.

△ four days water stress treatment.

▲ eight days water stress treatment.

** 1. Booting stage, 2.Heading stage, 3. Milk-repining stage, 4. Maturing stage.

低。

葉片澱粉含量變化(圖 2B)與硝酸還原酵素活性相似，唯各品系在抽穗期有最大澱粉含量，且以 80B 品系之澱粉含量較高。

圖 2C 係表示比葉重變化。80B 與臺中 5 號在乳熟期有最大比葉重，2R 之比葉重則隨生育期增加而增加；斷水處理時間愈長比葉重愈少；8 天斷水處理之比葉重在各品系差異不大。

淨同化作用速率與植株預存物質示於圖 3。80B 品系斷水 8 天處理在成熟期之淨化作用速率降至零，臺中 5 號及 2R 仍有些許淨同化作用速率存在。斷水 8 天在抽穗期有最大NAR。斷水 2 天，或對照組則在乳熟期有較大 NAR(圖 3A)。

80B 品系之預存物質隨生育時期增加而減少(圖 3B)，臺中 5 號及 2R 在乳熟期呈最大預存物質後下降，2R 在各生育期有較大預存物質表現。

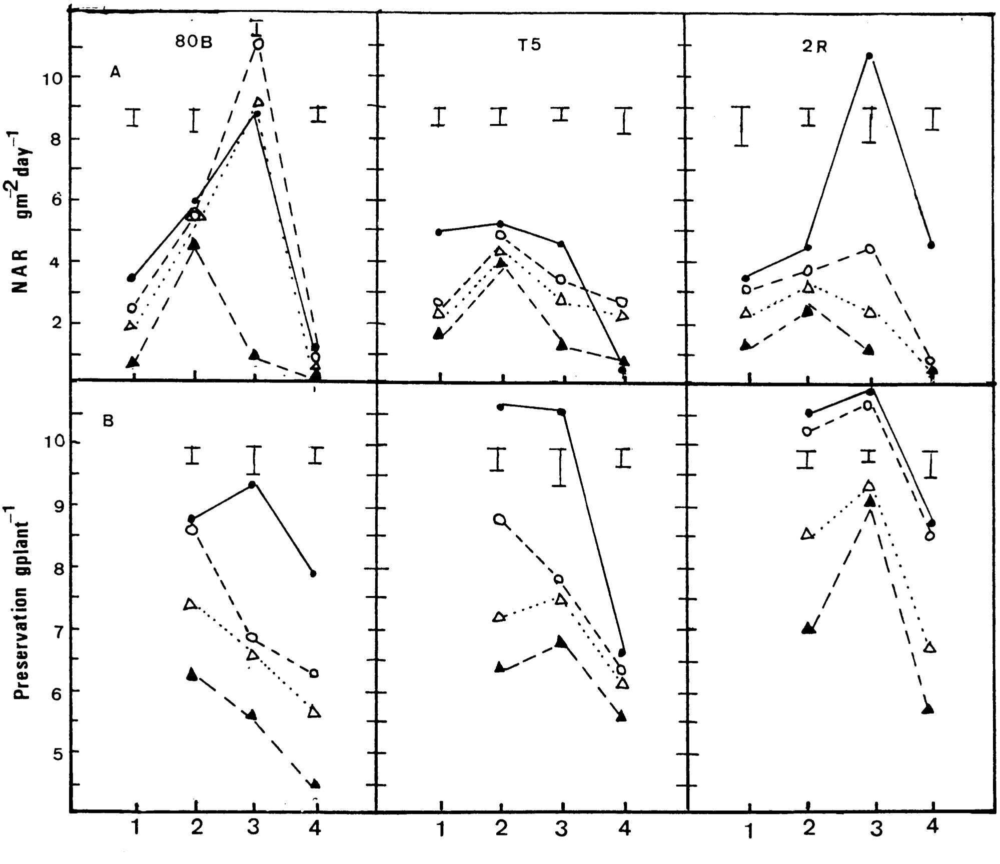

Fig 3. (A) NAR and (B)preservation of three sorghum genotypes under water stress treatment of different growth stage

* ● control.

○ two days water stress treatment.

△ four days water stress treatment.

▲ eight days water stress treatment

** 1. Booting stage, 2. Headint stage, 3. Milk-repining stage, 4. Maturing stage.

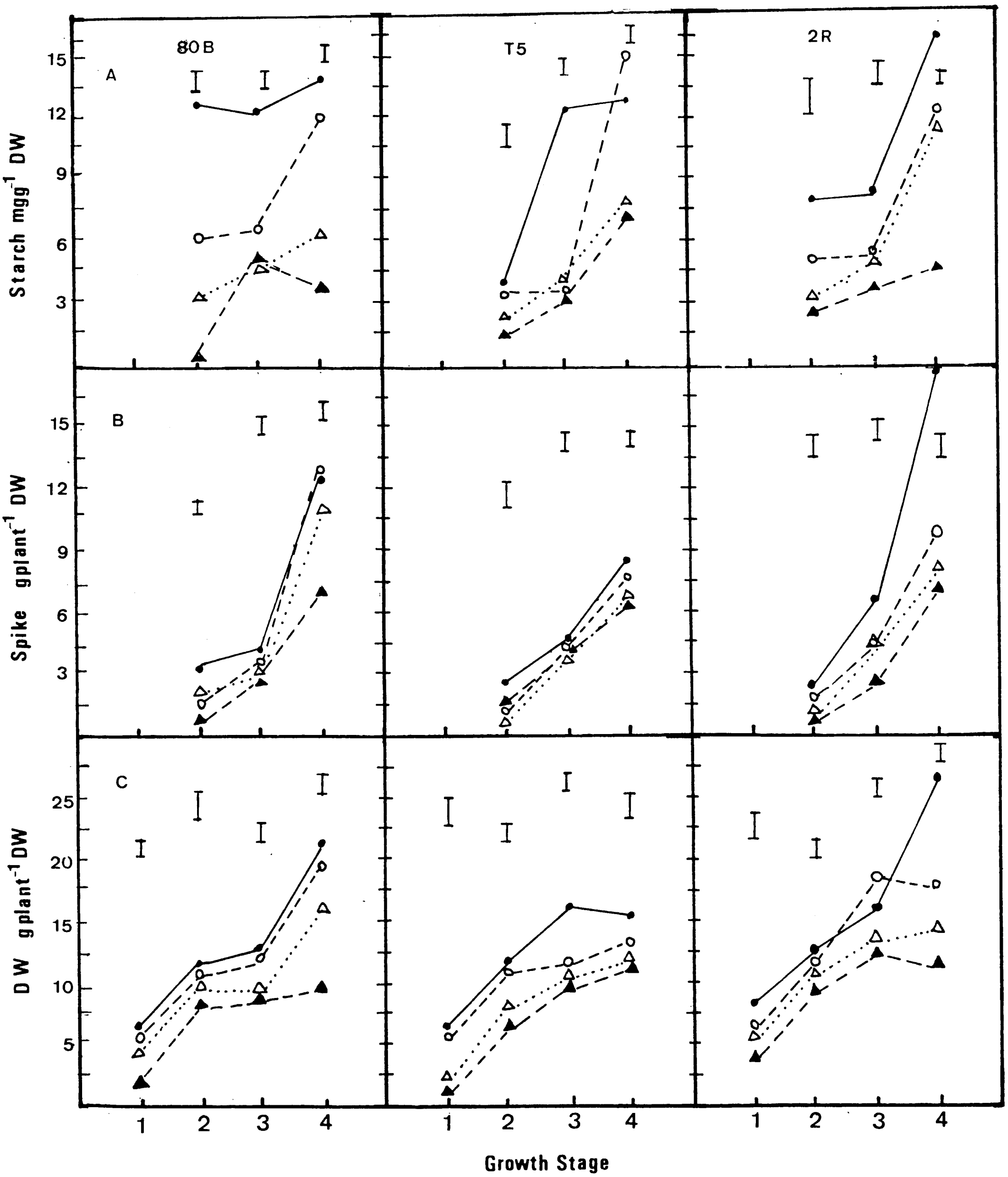

Fig 4. (A) Spike starch contents, (B) spike weight and (C) total dry weight of three sorghum genotypes under water stress treatment on different growth stages

* ● control.

○ two days water stress treatment.

△ four days water stress treatment.

▲ eight days water stress treatment

** 1. Booting stage, 2. Headint stage, 3. Milk-repining stage, 4. Maturing stage.

植株乾重變化示於圖4；乾重變化隨生育時期增加而增加，隨斷水時間加長而減輕，穗重與穗部澱粉含量亦呈類似變化。穗部澱粉含量2天及4天斷水處理。以2R有較大澱粉累積，8天斷水處理則以臺中5號有較多澱粉累積。

植株成熟時光合產物轉流情形示於表1，表中顯示對照組轉流物質較多，而斷水處理後，光合產物之轉流情形較少，植株體內現行產物仍多。各品系間以80B品系呈較大之轉流現象。

不同斷水處裡各品系於成熟期之農藝性狀表現示於表2。斷水處理後，穗長、穗數無明顯差異；穗重及小穗粒數及每穗種子重呈明顯差異存在。上述性狀皆隨斷水時間增長而減少，斷水8天後之穗重及每穗種子重以2R品系損失最爲嚴重，分別減少約爲80%與74%左右。

Table 1. The variation of photosynthetic assimilation under different water stress treatment for various sorghum genotypes.

Water stress treatment (day)	CAP* (%)			RE* (%)		
	2R	T5	80B	2R	T5	80B
Control	37.85b	59.87c	54.87b	62.16a	40.13a	45.14a
2	96.99a	79.42b	62.34b	3.01b	20.58b	37.66a
4	98.37a	86.94b	57.44b	1.63b	13.06b	42.56a
8	94.88a	98.22a	96.21a	5.13b	1.78c	3.79b

* CAP : current photosynthetic assimilation (100 - RE%);
RE : remobilization; measured at maturity stage.

Table 2. Effects of water stress treatment on the yield parameters of three sorghm genotypes.

Geno-type	Water stress treatment (day)	Height (cm)	Spike length (cm)	Spike no. per plant	Spike weight (g/plant)	Kernels no. per plant	Dry weight of seed per spike (g)
	Control	80.20 a	18.80 a	27.30 a	23.03 a	577.9 a	0.84 a
80B	2	80.90 a	18.70 a	26.50 a	23.30 a	596.5 a	0.88 a
	4	74.80 a	19.00 a	27.22 a	19.49 b	483.2 b	0.72 b
	8	59.20 b	16.90 a	25.70 a	13.45 c	435.1 b	0.52 c
	Control	86.30 a	13.40 a	27.40 a	16.34 a	384.0 a	0.60 a
TC5	2	188.35 a	13.30 a	26.25 a	11.61 b	278.2 b	0.44 b
	4	88.80 a	13.80 a	26.30 a	9.82 bc	220.0 bc	0.37 bc
	8	88.00 a	12.90 a	25.50 a	7.66 c	195.8 c	0.30 c
	Control	80.30 a	12.90 ab	26.70 a	15.59 a	401.9 a	0.58 a
2R	2	85.80 a	14.00 a	25.40 a	16.69 a	332.0 b	0.66 a
	4	65.00 b	14.10 a	26.40 a	9.07 b	293.0 b	0.34 b
	8	47.70 c	11.20 b	20.80 b	3.13 c	111.9 c	0.15 c

* Means with the same letter of a column are not different significantly according to Duncan's multiple range test (P=0.05).

葉片電導度與葉片水勢及滲透勢關係分別示於圖 5、6，顯示它們間並無相關關係存在。

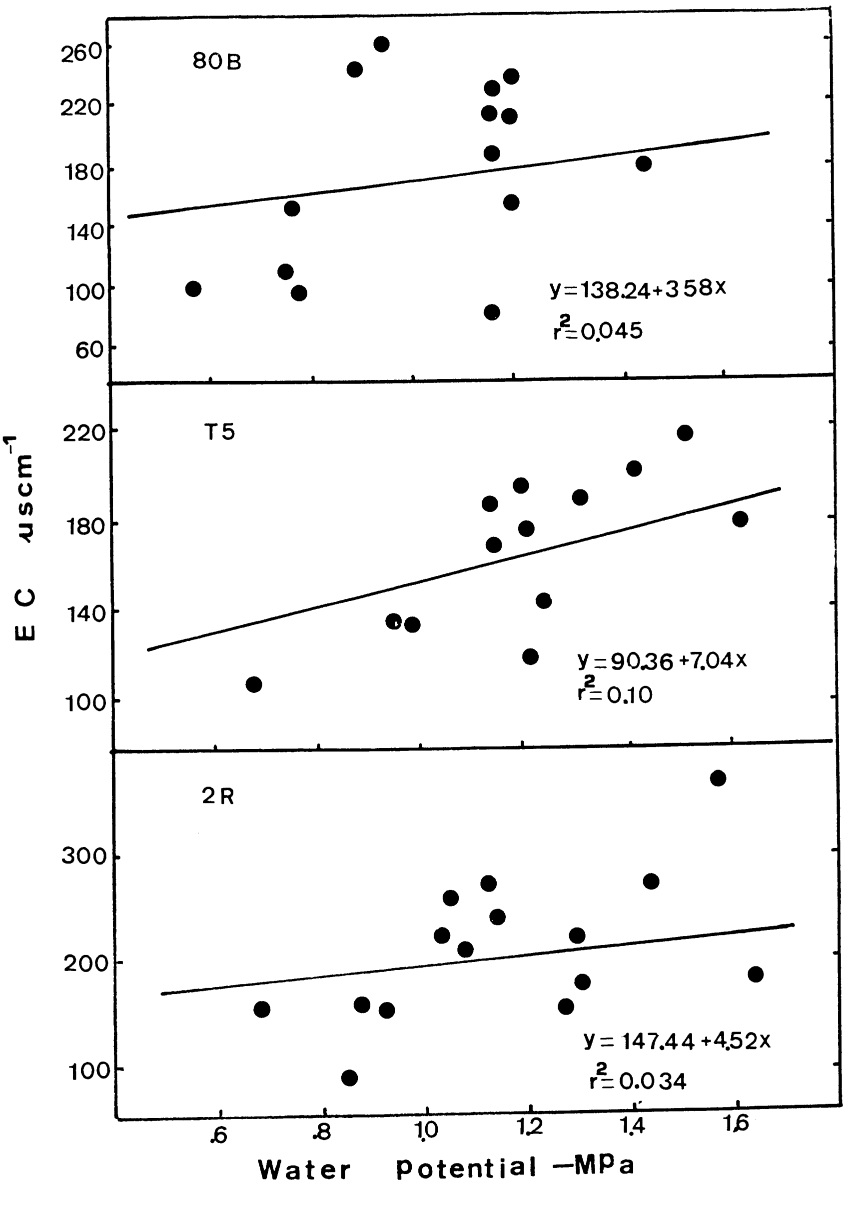

Fig 5. The relationships of regression of electric conductivity and water potential of three sorghum genotypes.

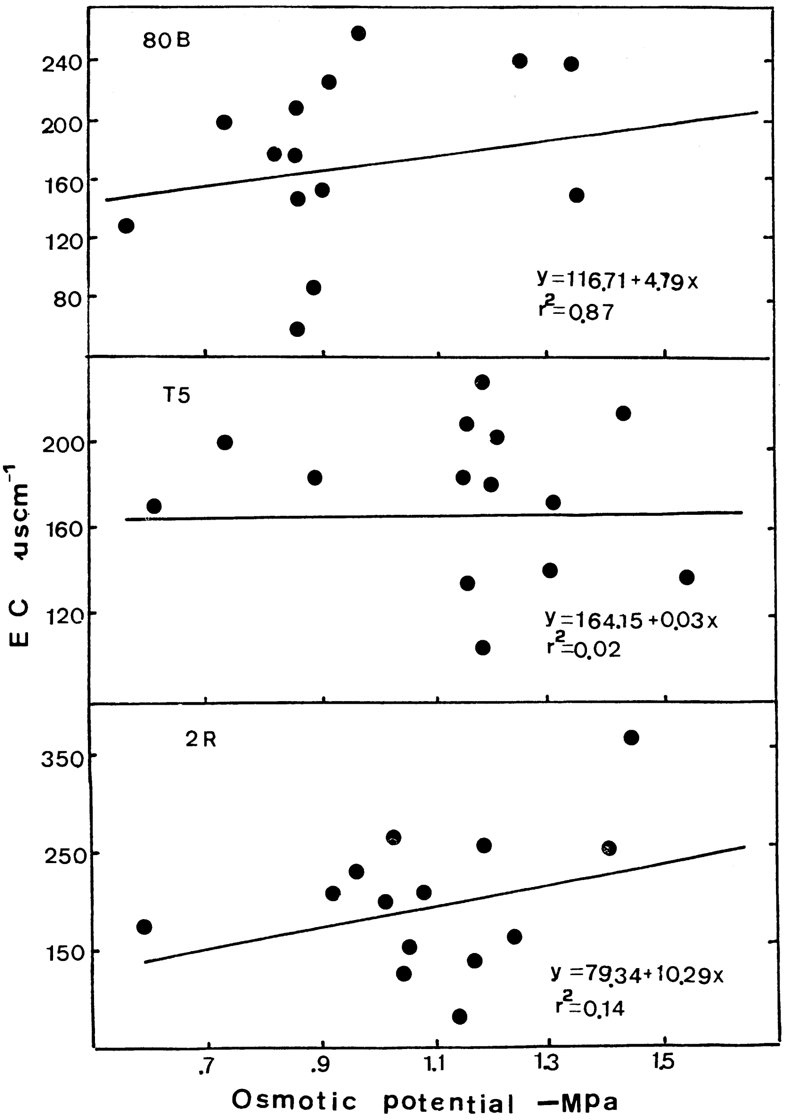

Fig 6. The relationships of electric conductivity and osmotic potential of three sorghum genotype.

討　論

作物基因型影響其生產能力，而環境逆境又可改變作物基因型。因此植物在其快速成長和發育階段中，對逆境之反應就顯得格外敏感。高粱雖屬耐旱作物，生殖期間缺水現象不僅影響其生殖器官發育 (Rosenthal and Gerik, 1989) ，亦影響其代謝過程 (Chaudhuri and Kanemasu, 1982)之表現。

一般而言，作物型態和其生理反應影響產量性狀表現；當作物有較大之葉面積，相對的其提供種子光合產物亦具較大之潛力 (Hogenboom et al., 1987a) ，缺水會使葉面積

減少(Ramseur et al., 1985；Rosenthal et al., 1987)，在本試驗中亦得相似結果(圖 1)，表示葉片伸展對土壤水分含量相當敏感(Rosenthal et al., 1987),且缺水促進老化作用進行(Cortes and Sinclair, 1986)，如硝酸還原酵素活性降低(Wolfe et al., 1988)，可溶性蛋白質含量減少(Irigoyen et al., 1992)等，在本試驗經斷水處理後發現葉綠素含量(圖 1C)，可溶性蛋白質含量(圖 1B)、硝酸還原酵素活性(圖 1A)、全糖及澱粉含量相繼減少(圖 2)，及影響產量性狀降低(表 2)，得到證實。Hoogenboom et al. (1987b) 提及缺水情況下，株高會影響作物之最終產量，唯本試驗不同品系不同斷水處理後株高差異表現並不相同(表2)，可能係受遺傳因子或溫度影響所致(Hoogenboom et al., 1987a)。

穀粒生長期間其所需之碳水化合物可能來自三處，一爲近前作物本身所進行之光合產物，一爲開花前儲存於基部或其他部位同化物之再轉流，另一則是開花後暫存於莖基部所轉運來之同化物(Kobata et al., 1992)。缺水降低同化作用限制供應穀粒之碳源，造成穀粒減少(Marks et al., 1985)；Wolfe et al. (1988) 謂開花前缺水會影響穗的發育，Ober et al. (1991)亦提及開花前缺水對穀粒數目發育有影響，而授粉後之缺水會影響穀粒發育大小；本試驗斷水處理後，穀粒內之內含物，穗重、穗粒數及稔實數顯著降低(表 2)，顯然缺水造成種子不育(Cox and Jolliff, 1986)及降低碳水化合物轉運到穀粒(Schussle and Westgate, 1991)。不斷水處理之植株其預存物質淨同化作用速率較多，(圖 3)，顯示其同化作用較强，有較多物質輸往子粒，可得較大種子充實速率；且其葉片有較重比葉重(圖 2)，表示有較大之光合作用能力(Kishitani and Tsunoda, 1982)，若植株在缺水下仍具較大比葉重者，表示可維持較好之水分平衡來穩定光合作用(Kishitani and Tsunoda, 1982)。

植物在缺水下，體內溶質累積是作物執行滲透調節之表現，以維持其本身生理活性(Cortes and Sinclair, 1987；Turner et al., 1987)，本試驗中由電導度值(圖 5、6)及葉片總糖含量增加(圖 2)得到證明，表示在低水勢下滲透勢明顯改變，可能係受葉片澱粉分解成可溶性糖類影響所致(Venekamp et al., 1989)；80B 品系在斷水 8 天後具較高總糖，澱粉及可溶性蛋白質含量，表示蛋白質被分解機率增大，及溶質提供滲透調節功能。物質提供滲調作用者，其對作物生長之貢獻亦較小，在 80B 乾重最小，得到證明。植株在斷水處理後，若仍在生育末期維持較高生理活性時(圖 1)，將有利於作物生產。

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The Effect of Water Stress on the Physiological Characteristic of Sorghum (*Sorghum bicolor* L.)

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Taichung No. 5, 2R and 80B were used in this study to investigate the physiological responses to water stress during reproductive stage of sorghum and their effects on yield. Two days, four days and eight days under water stress treatments were used on booting stage. The results showthat the leaf area, chlorophyll contents, soluble protein contents,nitrate reductase activity, starch contents and specific leaf weight (SLW) are decrease in accordance with the incease of time of water deficit treatment. Net assimilation rate (NAR) 、 preservation and and dry weightalso express same tendency. Whereas, total sugar contents of leaf express opposite responses. Different sorghum genotypes show diffent physiological responses on diffent growth stage under various water stress treatment. The genotype which maintain high physiological activity of the late growth stage will have better dry weight.

Key words : Sorghum, Water stress, Physiological response, Reproductive stage.